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CLADOCERA

Relationships among recent Alpine Cladocera remains and their environment: implications for climate-change studies

Christian Kamenik · Krystyna Szeroczyńska · Roland Schmidt

Abstract Our objective was to assess the potential of Cladocera from mountain lakes for climate reconstruction. We related Cladocera from surface sediments of Alpine lakes (1,502–2,309 m asl) to 29 abiotic environmental variables using statistical methods. The environmental dataset included water chemistry, lake depth, and bi-hourly water-temperature logs, which were used to assess mean monthly water temperatures, dates of freezing and breakup, spring and autumn mixing. We found 14 different Cladocera of the families Bosminidae, Daphniidae, and Chydoridae. Lakes without Cladocera (eight lakes) were cold and/or ultra-oligotrophic, whereas lakes with planktonic and littoral Cladocera (19 lakes) were warmer and/or less oligotrophic. Lakes with only littoral Cladocera (18 lakes) had intermediate water temperatures/trophy. Changes in Cladocera assemblages were related to changes in climate, nutrients, and/or alkalinity. We found a climate threshold at which Bosminidae disappeared in 95% of the lakes. For climate-change research, we propose studying Cladocera along transects that include climatic thresholds.

Keywords Lake mixing · Climate · Threshold · Alps · Mountain lakes

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C. Kamenik (✉)
Institute of Geography, University of Bern, Erlachstrasse 9a, Bern 3012, Switzerland
e-mail: christian.kamenik@giub.unibe.ch

K. Szeroczyńska
Institute of Geological Sciences, Polish Academy of Sciences, Twarda 51/55, Warsaw 00-818, Poland

R. Schmidt
Institute of Limnology, Austrian Academy of Sciences, Mondseestraße 9, Mondsee 5310, Austria

Introduction

Lake sediments are valuable climate archives (e.g., Moberg et al., 2005). Climate data beyond the instrumental period are essential to understand the climate system and to forecast future climate (Bradley, 2000). Sedimentary climate proxies, such as Cladocera, chironomids, diatoms, or chrysophyte remains, have been used to reconstruct climate throughout the Holocene, and beyond (e.g., Lotter et al., 2000; Heiri et al., 2003; Schmidt et al., 2004a; Kamenik & Schmidt, 2005). Combining the climate signals obtained from sedimentary proxies by using a 'multi-proxy approach' helps improving the reliability of climate reconstructions (Battarbee, 2000).

Cladocera (Crustacea) are an essential component of the zooplankton and littoral zoobenthos of mountain lakes (e.g., Winder et al., 2001; Manca & Armiraglio, 2002). Cladocera leave well preserved chitinous remains in lake sediments, which are often abundant

and diverse; and most of these remains can be identified to the specific level (Frey, 1986; Hofmann, 1987; Korhola & Rautio, 2001). Among the Cladocera preserved in lake sediments, Bosminidae and Daphniidae occur in the pelagic zone, while Chydoridae mainly represent littoral benthos (Frey, 1988). In north-temperate lakes, this habitat specificity was used to infer climate-related water-level changes (e.g., Sarmaja-Korjonen et al., 2003; Korhola et al., 2005). Contrary to this habitat specificity, Cladocera are not stenothermal (Meijering, 1983). Nevertheless, Cladocera assemblages were shown to respond to major climatic shifts, such as the Younger Dryas (e.g., Hofmann, 2000; Milecka & Szeroczyńska, 2005). They show changes along latitudinal and altitudinal gradients (e.g., Harmsworth, 1968; Lotter et al., 1997). In Norway and Finnish Lapland, altitude appeared to be the main factor driving crustacean species compositions, either directly via dispersal and colonization abilities or indirectly via temperature and the amount of aquatic vegetation (Sandøy & Nilssen, 1986; Rautio, 1998, 2001; Korhola, 1999). Lotter et al. (1997) and Korhola (1999) showed that air or water temperature had a statistically significant effect on Cladocera assemblages from Alpine and sub-arctic lakes sampled along steep ecoclimatic gradients, probably because the species differ in their temperature-tolerance. Cladocera were used for quantitative temperature reconstructions during the late-Glacial/early-Holocene (Duigan & Birks, 2000; Lotter et al., 2000).

Environmental changes that are not related to climate, such as eutrophication, acidification, or habitat modification, can hamper Cladocera-based climate reconstruction (e.g., Sarmaja-Korjonen & Alhonen, 1999; Duigan & Birks, 2000; Szeroczyńska, 2002; Hofmann, 2003). Besides climate and lake-level changes, Cladocera were shown to respond to e.g., variations in the acid–base balance, or in ion and nutrient concentrations (e.g., Lotter et al., 1997, 1998; Korhola, 1999). Changes in the catchment (e.g., deforestation) played a critical role for Cladocera assemblages during the Holocene (Lotter & Birks, 2003). Cladocera assemblages from five European mountain lakes showed only a weak or no response to air temperature during the last ca. 200 years (Battarbee et al., 2002). Battarbee et al. (2002) assumed that the Cladocera composition of these lakes was not sensitive to the range of temperature variation of the last 200 years. They hypothesized that Cladocera did not show climate-related changes, because the lakes selected in their study were not located near ecological boundaries or thresholds that were important for Cladocera.

The objective of this study was to assess the potential of Cladocera from lakes of the Niedere-Tauern (NT) area (Austrian Alps) for climate reconstruction. The lakes are located along an air temperature gradient; they are sensitive to climate change (Thompson et al., 2005). Instead of taking a single sample from the littoral and / or open water, we analyzed surface sediments from the deepest part of the lakes which integrate Cladocera over several years. This approach helped us avoiding bias introduced by the seasonal occurrence of Cladocera. Cladocera were related to the main underlying environmental gradients found among 29 abiotic variables using statistical methods. The significance of our findings with regard to Cladocera-based climate reconstruction is discussed.

Study area

We selected 45 lakes in the Central Alps (Niedere Tauern, Table 1) that stretch from the sub-alpine forested belt up to the mid-alpine zone (1,502−2,309 m asl). The altitudinal gradient reflects a major climate gradient with temperature decreasing with increasing altitude (Barry, 2001). Although the highest peaks rise above 2,800 m asl, there are no glaciers in the Niedere-Tauern. We particularly selected the region above 1,500 m asl, because lower mountain valleys tend to be affected by air-temperature inversions (Barry, 2001). The lakes were chosen to be as pristine as possible, while encompassing a wide spread of geographic settings, water chemistries, and basin morphologies. Their watersheds are located on predominantly crystalline bedrock with schists and metamorphic carbonates, which prevent them from being acidified. Table 2 lists summary statistics on physical, chemical, and morphometric characteristics.

Materials and methods

Cladocera analysis

Surface sediments (depth: 1 cm, diameter: 6 cm) were collected from the deepest areas of the 45 lakes

Table 1 Geographic position of the studied lakes and Cladocera found

Lake	No.	Longitude	Latitude	Altitude (m asl)	Cladocera
Ahornsee	1	13°59′03″ E	47°18′33″ N	2,069	Only littoral
Angersee	2	13°48′48″ E	47°17′22″ N	2,096	None
Eiskarsee	3	13°43′52″ E	47°17′00″ N	1,940	Only littoral
Elendbergsee	4	13°44′21″ E	47°17′00″ N	2,215	None
Grünsee	5	13°59′03″ E	47°17′14″ N	1,984	Only littoral
Hinterkarsee	6	13°54′23″ E	47°15′06″ N	2,074	Only littoral
Hohensee	7	14°00′31″ E	47°17′16″ N	1,541	Littoral and planktonic
Hüttensee	8	13°49′02″ E	47°21′30″ N	1,502	Only littoral
Hüttkarsee	9	13°54′18″ E	47°15′52″ N	2,137	Only littoral
Kaltenbachsee	10	13°47′12″ E	47°20′36″ N	2,214	None
Kapuzinersee	11	13°48′30″ E	47°17′46″ N	2,147	Only littoral
Knappenkarsee	12	13°40′29″ E	47°16′10″ N	2,257	Only littoral
Landauersee	13	13°40′00″ E	47°18′15″ N	1,653	Littoral and planktonic
Lungauer Klaffersee	14	13°47′55″ E	47°17′00″ N	2,196	None
Mitterkarsee	15	13°55′00″ E	47°14′36″ N	2,150	Littoral and planktonic
Mittlerer Kaltenbachsee	16	14°03′51″ E	47°16′55″ N	1,912	Littoral and planktonic
Mittlerer Landschitzsee	17	13°50′53″ E	47°15′00″ N	1,940	Only littoral
Moaralmsee	18	13°47′32″ E	47°21′28″ N	1,825	Littoral and planktonic
Oberer Giglachsee	19	13°38′36″ E	47°16′46″ N	1,930	Littoral and planktonic
Oberer Klaffersee	20	13°48′02″ E	47°17′34″ N	2,309	Only littoral
Oberer Landschitzsee	21	13°51′33″ E	47°14′49″ N	2,067	Littoral and planktonic
Oberer Landwiersee	22	13°43′13″ E	47°15′55″ N	2,047	Only littoral
Oberer Schönalmsee	23	13°36′04″ E	47°13′30″ N	2,111	Littoral and planktonic
Oberer Sonntagkarsee	24	13°49′53″ E	47°18′05″ N	2,063	Only littoral
Oberer Zwieflersee	25	14°02′39″ E	47°15′00″ N	1,925	Littoral and planktonic
Oberhüttensee	26	13°36′10″ E	47°16′43″ N	1,863	Littoral and planktonic
Obersee	27	13°49′06″ E	47°21′04″ N	1,672	Littoral and planktonic
Pfannsee	28	13°48′25″ E	47°21′00″ N	1,967	Littoral and planktonic
Rantensee	29	13°53′47″ E	47°15′00″ N	1,880	None
Rauhenbergsee	30	13°47′21″ E	47°17′41″ N	2,263	Only littoral
Schwarzensee	31	13°59′21″ E	47°17′26″ N	1,916	Only littoral
Tiefenbachsee	32	13°36′21″ E	47°14′25″ N	1,844	Littoral and planktonic
Twenger Almsee	33	13°36′05″ E	47°13′13″ N	2,118	Littoral and planktonic
Unterer Giglachsee	34	13°39′00″ E	47°17′00″ N	1,922	Littoral and planktonic
Unterer Kaltenbachsee	35	14°04′11″ E	47°16′41″ N	1,749	Littoral and planktonic
Unterer Klaffersee	36	13°47′36″ E	47°18′00″ N	2,103	Only littoral
Unterer Klaftersee	37	13°59′46″ E	47°19′00″ N	1,883	None
Unterer Landschitzsee	38	13°50′21″ E	47°15′18″ N	1,782	Littoral and planktonic
Unterer Landwiersee	39	13°43′29″ E	47°16′05″ N	1,978	Only littoral
Unterer Sonntagkarsee	40	13°49′46″ E	47°18′24″ N	1,962	Only littoral
Unterer Wirpitschsee	41	13°36′38″ E	47°14′06″ N	1,700	Littoral and planktonic
Unterer Zwieflersee	42	14°03′12″ E	47°14′54″ N	1,808	Littoral and planktonic
Weißensee	43	13°58′44″ E	47°18′47″ N	2,226	Only littoral
Wildlochsee	44	13°49′00″ E	47°20′00″ N	2,108	None
Zwerfenbergsee	45	13°48′38″ E	47°17′07″ N	2,025	None

Table 2 Summary statistics of 29 environmental variables from 45 lakes

Variable	Abbrev.	Units	Summary statistics			Principal components		
			Min	Median	Max	Axis 1	Axis 2	Axis 3
Climate-related variables								
Mean monthly June water temperature	T_{Jun}	Celsius	0.0	4.7	9.1	**−0.85**	−0.30	−0.25
Mean monthly July water temperature	T_{Jul}	Celsius	1.7	9.0	12.4	**−0.90**	0.07	−0.19
Mean monthly August water temperature	T_{Aug}	Celsius	6.1	10.7	13.7	−0.69	0.47	−0.19
Mean monthly September water temperature	T_{Sep}	Celsius	4.7	7.6	9.5	**−0.76**	0.38	−0.28
Mean monthly October water temperature	T_{Oct}	Celsius	1.5	4.8	6.2	**−0.83**	0.17	−0.28
Date of ice-break	Break	Julian days	118	146	198	**0.73**	0.41	0.29
Date of freeze-up	Freeze	Julian days	286	305	326	−0.66	0.17	−0.28
Length ice cover	Ice	Julian days	163	205	277	**0.80**	0.27	0.32
'Date of spring mixing'	S_{mix}	Julian days	133	158	264	**0.76**	0.18	0.35
'Date of autumn mixing'	A_{mix}	Julian days	262	294	303	**−0.79**	0.07	−0.16
Altitude	Alt	m asl	1502	1978	2309	**0.78**	0.33	0.23
Chemical variables								
pH	pH		6.9	7.2	8.2	−0.48	0.30	**0.75**
Alkalinity	Alk	μeq l^{-1}	22.0	131.5	1364.0	−0.59	0.04	**0.75**
Conductivity	Cond	μS_{25} cm^{-1}	11.9	25.9	137.3	−0.59	−0.08	**0.79**
Calcium	Ca	μeq l^{-1}	70.1	198.7	1058.8	−0.53	−0.11	**0.80**
Magnesium	Mg	μeq l^{-1}	10.5	21.6	303.8	−0.69	0.18	0.61
Sodium	Na	μeq l^{-1}	9.7	17.5	32.4	−0.36	−0.69	0.19
Potassium	K	μeq l^{-1}	3.4	8.2	21.0	0.18	−0.58	−0.25
Chloride	Cl	μeq l^{-1}	1.7	2.8	4.8	−0.57	−0.34	0.04
Sulfate	SO_4	μeq l^{-1}	28.7	71.2	295.8	−0.14	−0.48	0.56
Total inorganic nitrogen	TIN	μeq l^{-1}	0.0	9.0	18.1	0.22	**−0.74**	−0.08
Total dissolved nitrogen	DN	μg l^{-1}	82	234	397	0.23	**−0.72**	−0.03
Total phosphorus	TP	μg l^{-1}	1.0	3.2	7.8	−0.16	0.61	−0.08
Total particulate phosphorus	PP	μg l^{-1}	0.1	1.5	6.4	0.01	0.44	−0.19
Total dissolved phosphorus	DP	μg l^{-1}	0.2	1.4	3.3	−0.52	0.29	0.20
Total dissolved reactive silica	DRSi	μg l^{-1}	279	762	1,685	−0.20	**−0.85**	−0.11
Dissolved organic carbon	DOC	mg l^{-1}	0.41	0.60	2.06	−0.39	0.47	−0.46
Lake morphometry								
Maximum lake depth	z_{max}	m	5.7	13.4	43.6	0.08	0.36	−0.01
Relative lake depth[a]	z_{rel}	m	3.0	6.1	17.9	0.40	0.37	0.15
Amount of variance in the environmental data explained by Principal Components axes:						33%	18%	15%

Correlation coefficients indicate the measure of fit with significant Principal Component (PC) axes 1–3 (broken stick model). Scores >0.7 are presented in boldface. PC-axes 1–3 represent three major environmental gradients related to climate, nutrients, and alkalinity. Pfannsee was excluded from PC analysis because it lacked chemical measurements. PC-sample scores are shown in Fig. 1

[a] Lake area (m^2)/maximum lake depth (m)

during summer 1999 using a modified Kajak gravity corer. Samples (5 g wet sediment) were cleaned following Frey (1986): (i) removal of carbonates using HCl (10%); (ii) heating and stirring in KOH (10%) for 30 min to remove organic matter; (iii) washing and sieving (40 µm) of the residue, which was then diluted with distilled water (up to 10 ml), and mounted onto light-microscope slides (0.1 ml per slide). A minimum of 200 individuals per sample were counted (3−10 slides per sample). Their remains (headshields, shells, postabdomens, and postabdominal claws, excluding ephippia) were analyzed at 100× and 200× magnification using an OLYMPUS light microscope. The arrangement of fragmented remains into species followed Frey (1986). Cladocera taxonomy followed Goulden & Frey (1963), Frey (1964, 1991) and Flössner (1972, 2000).

Environmental variables

Kamenik et al. (2001) and Schmidt et al. (2004a, b) set out the details of the training set measurements. The survey involved water temperature, lake morphology, and water chemistry (Table 2) measured at the lake-centers (2 m water depth) on 18th/19th October 1999, i.e., around the time of autumn mixing (8th October–10th November 1999), when chemical characteristics tend to be similar throughout the water column. We avoided measuring water chemistry around the time of spring mixing, because chemical features can be highly variable during this period (Catalan et al., 2002). Epilimnion water-temperatures were measured at two-hour intervals using one or two 8-bit MINILOG-TR thermistors (Vemco Ltd.) per lake. Thermistors were exposed off the shore from summer 1998 to summer 1999. Temperature readings were averaged for the months June–October (T_{Jun}–T_{Oct}). Schmidt et al. (2004a, b) estimated freeze and breakup dates for each lake by visual examination of individual temperature logs. The reference dates 'date of spring mixing' (S_{mix}) and 'date of autumn mixing' (A_{mix}) were defined as the first day after thawing or summer stratification when the mean daily water temperature was 4°C (Schmidt et al., 2004b).

Numerical methods

The Cladocera counts were converted to presence/absence or percentages. Cladocera data were thus independent from changes in sediment characteristics. Percentages were square-root transformed to stabilize their variance. We did not perform 'down-weighting of rare species' (ter Braak & Šmilauer, 2002), because maximum abundance was always $\geq 3\%$, and because downweighting would have resulted in a weighting of 50% of the species. Cladocera assemblages were compared using a dissimilarity index (Chord distance), and grouped according to Non-Metric Multidimensional Scaling (MDS) and Hierarchical Agglomerative Clustering (UPGMA) (Legendre & Legendre, 1998). Cladocera that characterized specific groups of lakes were identified using the indicator-value approach (Dufrêne & Legendre, 1997). The significance of indicator values was assessed by randomization (999 permutations).

Main patterns in the environmental variables and the corresponding lakes were elucidated by Principal Components (PC) analysis (Table 2, Fig. 1) after data were centered and standardized (Legendre & Legendre, 1998). The significance of PC-axes was assessed by the broken stick model (Jackson, 1993). Isolines of environmental variables were projected onto a PC-plot using generalized additive models with PC-axes 1 and 2 as predictors, a normal error structure and an identity link function (Venables & Ripley, 2002; Lepš & Šmilauer, 2003). All environmental variables, except pH (i.e., $-\log_{10}[H^+]$), were $\log_{10}$ transformed to avoid skewed distributions. Linear relationships between $[H^+]$ and other ions were thus retained (Stumm & Morgan, 1996).

We used a Classification Tree and Canonical Variates Analysis (also known as Linear Discriminant Analysis) to analyze relationships between the presence/absence of Cladocera and environmental variables (Venables & Ripley, 2002), and Canonical Correspondence Analysis to study potential effects of these variables on the Cladocera assemblages (Legendre & Legendre, 1998). A preliminary Detrended Correspondence Analyses (DCA, detrending by segments) on the Cladocera assemblages resulted in a gradient length of 2.4 standard deviation units, suggesting unimodal species responses (ter Braak, 1987; Birks, 1995). DCA and CCA helped identifying outlying samples (ter Braak, 1987). A series of Detrended Canonical Correspondence Analyses (DCCA) constrained to a single environmental variable at a time were run to check the influence of each

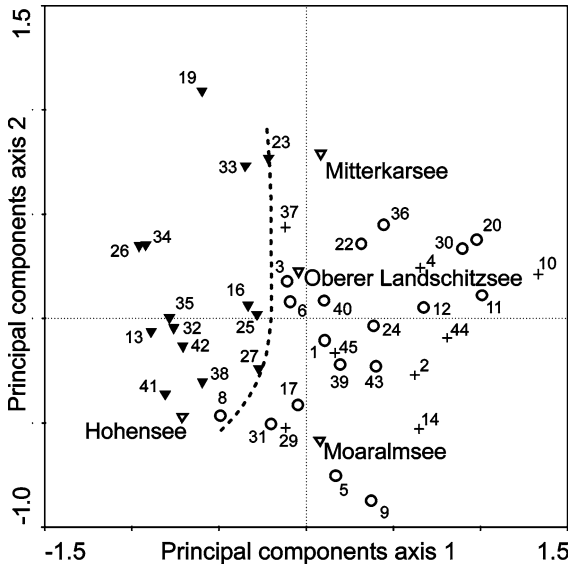

Fig. 1 Surface-sediment sample-scores from a PCA based on 44 lakes (Table 1) and 29 abiotic variables (Table 2). The samples are grouped in lakes (i) that lack Cladocera (crosses), (ii) that have only littoral Cladocera (circles), and (iii) that have littoral and planktonic Cladocera (triangles). The transition from lakes with planktonic Cladocera to lakes without planktonic Cladocera is related to a 'date of autumn mixing' of 297 Julian days (dashed line, fitted by GAM, $P < 0.001$). Black and white fillings reflect results from numerical clustering, and agree with the occurrence of Cladocera, except for the four-labeled lakes (for numbering see Table 1). Significant PC-axis 3 did not separate lakes with Cladocera from lakes without Cladocera. Pfannsee was excluded because it lacked chemical measurements

variable on the Cladocera assemblages (marginal effects). DCCA helped assessing the gradient length of the environmental variable in standard deviation (SD) units (turnover units of beta-diversity). Using DCCA, we determined the strength of each variable by its ability to maximize the dispersion of the taxon scores (ter Braak & Juggins, 1993), expressed as a ratio of the eigenvalue of the constrained ordination axis to the eigenvalue of the first unconstrained ordination axis (λ_1/λ_2).

We used PC-axis 1 sample-scores (see Table 2) as an index for climate; PC-axis 1 was highest correlated with climate-related variables (compare with Thompson et al., 2005). Furthermore, we used PC-axis 2 and 3 sample-scores as indices for nutrients (e.g., from pastures) and alkalinity supply (e.g., from weathering of bedrock minerals); they were highly correlated with nitrogen fractions and alkalinity, respectively (compare with Kamenik et al., 2001). Because PC axes are not correlated (e.g., Legendre & Legendre, 1998), the three indices were independent from each other. The significance of explanatory variables, of individual CCA and DCCA axes, and of the tree-based statistical classification model was tested using 999 unrestricted permutations (ter Braak & Šmilauer, 2002). To eliminate spurious marginal effects, we adjusted their probability values for multiple testing ($P_{adj} < 0.05$) using the conservative Bonferroni correction (Wright, 1992).

Finally, we used the optimal sum-of-squares partitioning method (Birks & Gordon, 1985), as implemented in the program ZONE (Lotter & Juggins, 1991), and the broken-stick model (Bennett, 1996) to detect significant changes among Cladocera assemblages along environmental gradients of interest.

Bivariate statistical analysis followed Venables & Ripley (2002) and Venables & Smith (2002) using the R language. Ordinations (PCA, CVA, DCA, CCA, DCCA) were calculated using the program CANOCO 4.5 (ter Braak & Šmilauer, 2002). For MDS, cluster analysis, and the tree-based statistical classification model we used the R-libraries CLUSTER, MASS, RPART, and RPART.PERMUTATION (Venables & Ripley, 2002; Cummings et al., 2004). Indicator values were calculated using the program IndVal (Dufrêne & Legendre, 1997).

Results

General characteristics

We found 14 different Cladocera of the families Bosminidae, Daphniidae, and Chydoridae. Shells and head shields were the most abundant remains. Unknown remains were discovered in Unterer Wirpitschsee and nearby Tiefenbachsee. In eight lakes no Cladocera could be found (Figs. 1, 2). In lakes with Cladocera, we found one (*Alona affinis* in Weissensee) to nine (Hohensee) species. Planktonic Cladocera (*Daphnia longispina*-group, *D. pulex*-group, *Bosmina* (*Eubosmina*) type, and *Bosmina longirostris*) were found in 19 lakes (Figs. 1, 2). The littoral Cladocera *Alona affinis* and *Acroperus harpae* had the highest number of occurrence (we found *A. affinis*

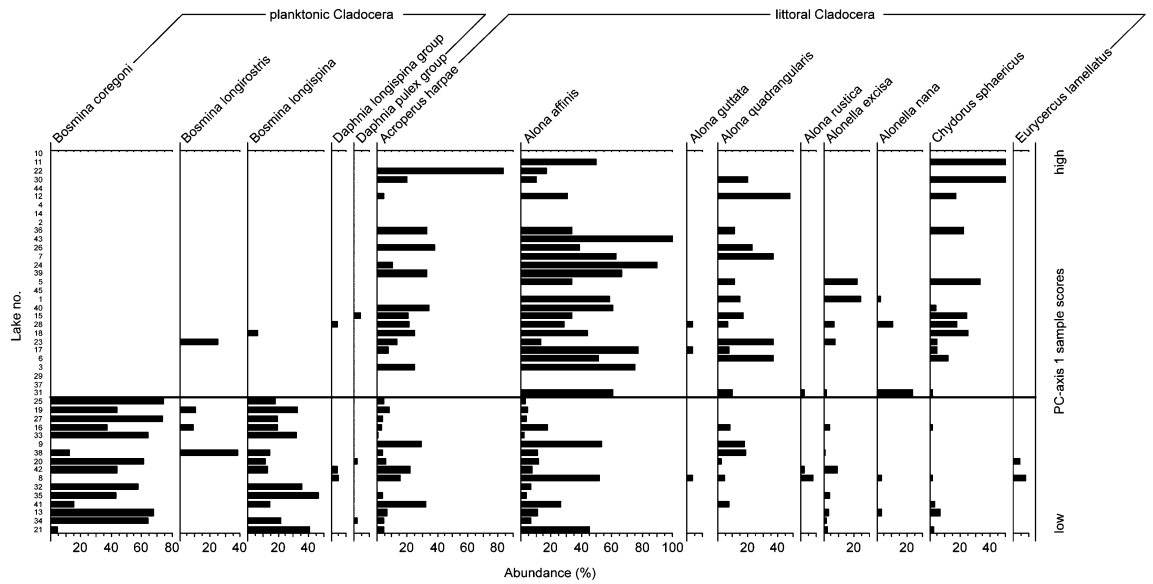

Fig. 2 Abundance of Cladocera ordered along PC-axis 1 sample-scores; the horizontal line indicates a significant change in the Cladocera assemblages according to optimal partitioning (based on Cladocera percentages) and the broken stick model, and corresponds to e.g., a 'date of autumn mixing' of 297 Julian days (Fig. 1). Low/high sample scores denote warm/cold lakes, respectively. Pfannsee (no. 28), which lacked chemical measurements, was inserted according to (i) a PCA on climate-related variables and lake morphology (Table 2) and (ii) similarity among Cladocera assemblages (cluster analysis)

in 37 and *A. harpae* in 29 lakes), followed by *Alona quadrangularis* and *Chydorus sphaericus* (both found in 19 lakes). The total number of Cladocera fluctuated around 200 per gram wet sediment (median value). The maximum concentration of Cladocera was 1,850 per gram wet sediment in Obersee.

Detrended Correspondence Analysis (DCA) did not indicate unusual Cladocera assemblages. MDS, cluster analysis, and the indicator value approach revealed that there were two different groups of Cladocera assemblages that were characterized either by planktonic Cladocera (*Bosmina coregoni*, *Bosmina longirostris*) or by littoral Cladocera (*Alona affinis*, *Alona quadrangularis*, *Chydorus sphaericus*). The former group included all lakes with planktonic Cladocera except for Hohensee, Mitterkarsee, Moaralmsee, Oberer Landschitzsee, and Pfannsee (Fig. 1). These lakes had either a high abundance of *Alona quadrangularis* (Oberer Landschitzsee) or low abundances (<7%) of planktonic Cladocera (Fig. 2).

A classification tree suggested that at mean August water temperature (T_{Aug}) < 8.9°C no Cladocera could be found (misclassifying Grünsee, Elendbergsee, Rantensee, Unterer Klaftersee, and Zwerfenbergsee); the same classification tree suggested that at mean October air temperature (T_{Oct}) > 5.1°C there were both littoral and planktonic Cladocera in the surface sediments (misclassifying Hüttensee, Mitterkarsee, Moaralmsee, and Pfannsee). Canonical Variates Analysis (CVA) revealed that Zwerfenbergsee could not be classified correctly even when considering all 29 environmental variables. T_{Oct} had highest correlation with 'date of autumn mixing' (Kendall's $\tau = 0.82$). The 'date of autumn mixing' isoline of 297 Julian days separated lakes with planktonic Cladocera from lakes without (overall significance of the underlying GAM model according to *F*-statistics: $P < 0.001$). Hüttensee, Mitterkarsee, Moaralmsee, and Oberer Landschitzsee were misclassified in the PC-plot (Fig. 1). Pfannsee was excluded from PCA and CVA because it lacked chemical measurements.

Correlations of Cladocera assemblages with environmental variables

Ten environmental variables and PC-axis 1, which was highly correlated with climate-related variables, had significant marginal effects (taking into account multiple testing). They explained 9.1–15.1% of variation among the Cladocera assemblages

Table 3 DCCA results, based on Cladocera percentages, listing environmental variables, and PC-sample scores (Table 2), which singly explained a significant amount of variation in the Cladocera assemblages found in 37 lakes (marginal effects)

	Percentage of variation explained	λ_1/λ_2	Gradient length
'Date of autumn mixing'	15.1	0.88	1.8
PC-axis 1 sample-scores	15.0	0.85	1.8
Magnesium	14.7	0.87	1.7
Mean monthly October water temperature	14.4	0.84	2.1
Mean monthly September water temperature	12.1	0.61	1.7
Alkalinity	10.8	0.62	1.7
Total phosphorus	10.8	0.67	1.7
Mean monthly July water temperature	10.7	0.47	1.6
pH	10.6	0.58	1.6
Total dissolved phosphorus	10.3	0.51	1.8
Conductivity	9.6	0.52	1.5

PC-sample scores were used as indices for climate (axis 1), nutrients (axis 2), and alkalinity supply (axis 3). λ_1/λ_2 show the strength of each variable by its ability to maximize the dispersion of the taxon scores. High values indicate strong secondary gradients. Gradient lengths, given in turnover units of beta-diversity, show the amount of compositional change along the variables

(Table 3). 'Date of autumn mixing' explained most of the variation. According to DCCA, the amount of compositional change along these variables ranged from 1.5 to 2.1 standard deviation (SD) units (turnover units of beta-diversity). DCCA indicated strong secondary gradients ($\lambda_1/\lambda_2 < 0.9$). Optimal partitioning and the broken-stick model revealed that along PC-axis 1 there was a significant change in the Cladocera assemblages. This change mainly denoted a shift from assemblages characterized by planktonic Cladocera to assemblages characterized by littoral Cladocera (Fig. 2).

CCA based on the three PC axes, which summarized the main underlying gradients in the environmental variables (Table 2), resulted in two significant canonical correspondence axes, which explained 24.8% of the variation in the Cladocera assemblages. The three PC-axes sample-scores had significant conditional effects (i.e., they significantly explained additional variation in the Cladocera assemblages after other PC axes had been considered). PC-axis 1 sample-scores were highest correlated with canonical correspondence axis 1; PC-axis 3 sample-scores were highest correlated with canonical correspondence axis 2 (Table 4).

Canonical correspondence axis 1 separated lakes with planktonic Cladocera from lakes without planktonic Cladocera. According to their Indicator Values, the three Bosminidae characterized warm/nutrient-rich lakes; in turn, *Alona affinis* and *Chydorus sphaericus* characterized cold/nutrient-poor lakes. The first unconstrained axis explained a high amount of variation in the Cladocera assemblages (Table 4). Hohensee, which is a shallow lake (z_{rel} = 3.0 m) at an altitude of 1,541 m asl, was an outlier on this first unconstrained axis (sample-score >2.5× higher than the interquartile range of all sample scores).

Discussion

General characteristics

The main compositional change in Cladocera assemblages from Swiss lakes located along an altitude gradient ranging from 334 m asl to 2,339 m asl occurred between 1,000 m asl and 1,500 m asl (Lotter et al., 1997). The NT-Cladocera assemblages were all sampled from lakes located above 1,500 m asl. They were mainly characterized by cold-tolerant planktonic (Bosminidae, Daphniidae) and littoral (Chydoridae) Cladocera.

The most frequent Cladocera from the NT-sediments were Chydoridae that were classified as either 'arctic' (*Acroperus harpae*, *Chydorus sphaericus*), 'sub-arctic' (*Alona affinis*) or 'north-temperate' (*Alona quadrangularis*), according to their occurrence at high-latitude sites (Harmsworth, 1968).

Table 4 CCA (summary) based on percentages of 14 different Cladocera, 35 samples and sample-scores derived from a PCA on environmental variables (Table 2) which were used as indices for climate (axis 1), nutrients (axis 2), and alkalinity supply (axis 3)

Canonical correspondence axes:	1	2	3	First unconstrained axis
Eigenvalues	0.31	0.12	0.04	0.30
Species environment correlations	0.79	0.74	0.62	0.00
Cumulative percentage of variance				
of species data	17.8	24.8	27.4	44.6
of species–environment relationship	65.1	90.7	100.0	0.00
Significance of axis (probability)	0.001	0.019	0.706	Not available
Inter set correlations of environmental variables with axes				
PC-axis 1 sample-scores	**−0.69**	**0.32**	−0.14	Not available
PC-axis 2 sample-scores	**0.31**	**0.39**	**−0.47**	Not available
PC-axis 3 sample-scores	0.25	**0.57**	**0.34**	Not available
Sum of all eigenvalues				1.72
Sum of all canonical eigenvalues				0.47

Inter-set correlations of variables with significant canonical coefficients are presented in boldface (approximate *t*-value >2.1)

During the Late-Glacial and earliest Post-Glacial, 'arctic and sub-arctic' Cladocera were often found to be pioneer taxa, i.e., early immigrants after ice withdrawal (e.g., Szeroczyńska, 1998a; Duigan & Birks, 2000; Hofmann, 2000, 2001). The high number of occurrences of these Cladocera in the NT-lakes suggests that they should, however, not be regarded as cold stenothermal but as cold tolerant (Meijering, 1983). *Alona affinis* and *Chydorus sphaericus*, for example, are known to occur over a wide range of environmental conditions (e.g., Duigan & Kovach, 1991; Duigan, 1992; Korhola, 1999).

Planktonic Cladocera were dominated by Bosminidae (*Bosmina coregoni* and *B. longispina*), which occurred in 'warm' and/or 'nutrient-rich' NT-lakes. Bosminidae were absent in oligotrophic mountain lakes in the Tatra Mountains (Szeroczyńska, 1984). Lotter et al. (1997) and Hofmann (2003) showed that Bosminidae played a minor role in the plankton of Swiss lakes above 1,800 m asl. Percentages of *Bosmina* sp. were shown to increase during climate amelioration or nutrient input (Harmsworth, 1968; Duigan & Birks, 2000; Szeroczyńska, 2002; Gąsiorowski & Szeroczyńska, 2004). However, like the previously mentioned Chydoridae, *Bosmina coregoni*, *B. longirostris*, and *B. longispina* are known to occur over a wide range of environmental conditions (Frey, 1988; Korhola, 1999; Gąsiorowski & Szeroczyńska, 2004).

It is difficult to speculate upon the reasons for the absence of Cladocera in eight of the lakes. A classification tree suggested that water temperature was a driving force. Misclassifications revealed, however, that the absence of Cladocera is governed by a complex interplay of environmental factors. Unmeasured variables, such as poor preservation, oxygen concentration, water-transparency, damage by ultraviolet radiation, competition, grazing, food availability and predation, may strongly influence the Cladocera distribution (e.g., Hofmann, 1987; Whiteside & Swindoll, 1988; Szeroczyńska, 1998b; Korhola, 1999; Williamson et al., 2001; Jeppesen et al., 2003).

Correlations of Cladocera assemblages with environmental variables

Direct gradient analysis (CCA, DCCA) stressed the importance of climate-related environmental variables for the Cladocera assemblages of the NT-lakes; however, instead of a gradual change along the climate gradient, we found a climate threshold at which we discovered a significant change in assemblage composition (Figs. 1, 2).

The strong climate-related change in Cladocera assemblages can be the result of both direct and indirect temperature effects (Lotter et al., 1997; Korhola, 1999). Temperature determines, for example, the inter-moult duration, which is intimately linked to the growth of Cladocera (Bottrell, 1975). Hofmann (2000) noted that the distribution of

Cladocera did not always coincide with their thermal classification. Hofmann (2003) suggested that changes in the chydorid fauna in the Swiss-mountain Lake Sägistalsee (1,935 m asl) were related to improved light conditions, which favored the submerged vegetation and therefore increased the diversity of the littoral habitat. Rautio (1998, 2001) suggested that the length of the growing season affects Cladocera via modifying the occurrence of macrophytes. Whiteside and Harmsworth (1967) and Whiteside and Swindoll (1988) suggested that the complexity of the littoral habitat is reflected in Chydorid diversity. The strong secondary gradients in the NT-Cladocera assemblages (λ_1/λ_2 in Table 3), which were not related to any measured environmental variable, are probably correlated with habitat structure. Hohensee, which had the highest sample scores along the unconstrained ordination axes in DCCA or CCA (Tables 3, 4), was found to have a well-developed macrophyte community covering almost the entire lake bottom (pers. observation).

Although shifts from planktonic to littoral Cladocera were used to reconstruct lake-level changes in northern-temperate kettle-hole lakes (Korhola et al., 2005), this does not necessarily mean that Cladocera assemblages are correlated with mean or maximum depth, area, or volume of the lakes (Hofmann, 1996; this study). Cladocera that cannot strictly be assigned to either planktonic or littoral species, such as *Chydorus sphaericus*, may distort any correlation between water depth and Cladocera assemblages (Müller, 1964). More importantly, Cladocera-based lake-level models are based on the observation that the extension of the littoral area, rather than mean or maximum depth, affects the ratio between planktonic and littoral Cladocera (Hofmann, 1998).

The growth of zooplankton may be constrained by the availability of carbon, calcium, and phosphorus (Urabe et al., 1997; Schulz & Sterner, 1999). We found that the occurrence of *Daphnia* sp. in the NT-lakes was associated with high DOC concentration. Hessen and Rukke (2000) suggested that a high seston carbon to phosphorus ratio in combination with low calcium could cause a marked reduction in production of *Daphnia.* This could shift the competitive advantage toward less phosphorus and calcium demanding species. Winder et al. (2001) reported that chlorophyll a and particulate organic carbon best separated lakes with *Daphnia* from lakes without.

Bos and Cumming (2003) proposed that nutrients affected Cladocera assemblages via changes in habitat structure. According to Hofmann (1986), the littoral Cladocera do not react to an increase in trophy until the decrease in transparency limits the growth of macrophytes. Sterner et al. (1993) and Plath and Boersma (2001) suggested that changes in nutrients alter food availability and modify Cladocera assemblages. Mixing causes re-suspension of nutrients (Catalan et al., 2002). Phosphorus and calcium concentrations affect the molting process (Hessen & Rukke, 2000). Temperature, calcium, and phosphorus are therefore linked via build-up and loss of exuviae. Metabolic links may be reflected by the significant canonical correspondence axis 1 (Table 4) which summarized effects of climate and nutrients.

Besides climate, Cladocera are possibly affected by nutrient input from alpine pastures (e.g., Kamenik et al., 2000; Hausmann et al., 2002), as suggested by the presence of *Bosmina longirostris*, which is considered to be an indicator of eutrophic conditions (e.g., Harmsworth, 1968; Gąsiorowski & Szeroczyńska, 2004). During summer, all lakes with *B. longirostris* had cows in their catchments.

PC-axis 3, which was used as index for alkalinity supply, significantly explained variation in the Cladocera assemblages that was independent from the climate-related PC-axis 1 (Table 4). Lotter et al. (1997) showed that lake-water calcium concentration, which was linked to bedrock mineralogy and vegetation cover, best explained variation in Cladocera assemblages from the Swiss Alps. Bedrock mineralogy, which was independent of altitude and hence air temperature, was also the primary factor controlling cation availability in the NT-lakes (Kamenik et al., 2001). pH appears to affect Cladocera diversity only at levels that lie below the minimum pH found in the NT-lakes (Manca & Armiraglio, 2002).

Cladocera-based climate reconstruction

We found two distinctly different Cladocera assemblages in our study area that were characterized by the presence/absence of Bosminidae. The two assemblages were separated by a climate threshold. Commonly used inference models, such as weighted averaging or logistic regression, assume a unimodal species response along an environmental gradient; for reliable estimates of a species' optima and tolerance,

samples should be evenly distributed along this environmental gradient (ter Braak & Looman, 1986). Clearly, these assumptions are not fulfilled in our dataset.

Nevertheless, Cladocera may be valuable climate proxies. Shifts from assemblages with Bosminidae to assemblages without Bosminidae (and vice versa), observed in sediment cores taken along transects (e.g., different altitudes) that include climatic thresholds probably illustrate the direction and magnitude of climate change. The sensitivity of this approach would be determined by the spatial representation of lakes along the climate gradient. The Niedere-Tauern area appears to be suitable for such an approach, because the climate threshold is located near the center of the climate gradient (Fig. 1).

Conclusions

In mountain lakes, Cladocera appear to be primarily driven by climate-related variables. There seems to be a climate threshold which triggers changes in Cladocera assemblages. The link between Cladocera and climate may be direct (e.g., via changing metabolic rates) or indirect (e.g., via changes in habitat structure or food availability). If the link was indirect, climate-independent changes in nutrients, the acid–base balance, or habitat structure may cause artifacts in Cladocera-based climate reconstructions. In sum, we recommend Cladocera as a valuable tool for multi-proxy climate reconstructions. Study sites should be located near climate thresholds that are important for Cladocera.

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